The Benthic and Pelagic Habitats of the Red Crab, *Pleuroncodes planipes*

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IN MARCH 1895, several specimens of an undescribed anomuran crab were washed ashore at Monterey, California. These, along with some similar animals found in oceanic waters (24°N, 130°W), were sent to William Stimpson, who was describing the crustacean material collected by the North Pacific Exploring Expedition. Stimpson described both the Monterey and the high seas specimens as a new genus and a new species, *Pleuroncodes planipes*, assigned to the family Galatheidae (Stimpson, 1860). The "red crab" or "pelagic crab" (Fig. 1) is familiar to inhabitants of Baja California and occasionally is seen along southern California beaches, where large numbers of these animals are at times washed up and left stranded by receding tides. Their brilliant red coloration, together with their relatively large size, makes such occurrences of these animals a striking phenomenon. The present study was undertaken as an investigation into the pelagic distribution and possible benthic nature of the species; prior to this study *P. planipes* was believed to be only planktonic.

Members of the family Galatheidae are typically benthic when adult and are commonly known as "squat lobsters." Larvae of all the species are pelagic for at least a short time, and presumably the small postlarvae can alternate between the plankton and the benthos before assuming an exclusively benthic life. Two antarctic species, *Munida gregaria* (Fabricius) 1793 and *M. subrugosa* (White) 1847, may be either pelagic or benthic as adults, but are more commonly benthic (Matthews, 1932). The young of *M. gregaria*—the so-called Grimothea stage—are predominantly pelagic and have been reported on several occasions as so numerous that they color the sea bright red over large areas (Matthews, 1932; Bary, 1953). *P. planipes* probably has evolved from stock that was benthic, for of the 230 described species in the family Galatheidae only the two species of *Munida* discussed above and *P. planipes* are ever planktonic as adults.

In the new genus Stimpson also included a Chilean species described by Milne-Edwards (1837) as *Galathea monodon*, which hence became *Pleuroncodes monodon*; these are the only two species assigned to the genus at present. Initial descriptions of the two species are quite inadequate. Milne-Edwards' description of *G. monodon* morphologically fits most of the species of *Munida*, a large genus closely related to *Pleuroncodes* and containing about 41 species; however, his figures of *G. monodon*, published in 1851, are excellent. Stimpson's description of *P. planipes* (1860) is only slightly better; he did not present any figures of the new species, which apparently was first illustrated by Schmitt (1921). Schmitt's description of *P. planipes* is the most complete to date. *P. monodon* is described by Faxon (1895) and Haig (1955). The larval stages of *P. planipes* have been described in earlier papers (Boyd, 1960; Boyd and Johnson, 1963).

A fossil specimen probably belonging to *Pleuroncodes* was found by Carl L. Hubbs, of Scripps Institution of Oceanography (Miller, 1951). This specimen was from a sea cliff of the Capistrano Formation (an Upper Miocene deposit), about 1 mile south of Capistrano Beach, Orange County, California. It is not known whether the fossil was *P. planipes*, although the specimen was found well within the present-day distributional range of the species.

Specimens of *P. planipes* freshly taken by dipnet from the ocean surface immediately settle to the bottom of a shipboard aquarium and assume a benthic existence in sharp contrast to their pelagic life of a few moments earlier. Crabs kept in laboratory aquaria for growth studies lived almost entirely as benthic animals. It was believed that the question of whether the crabs were benthic in nature could not be answered conclusively by observations

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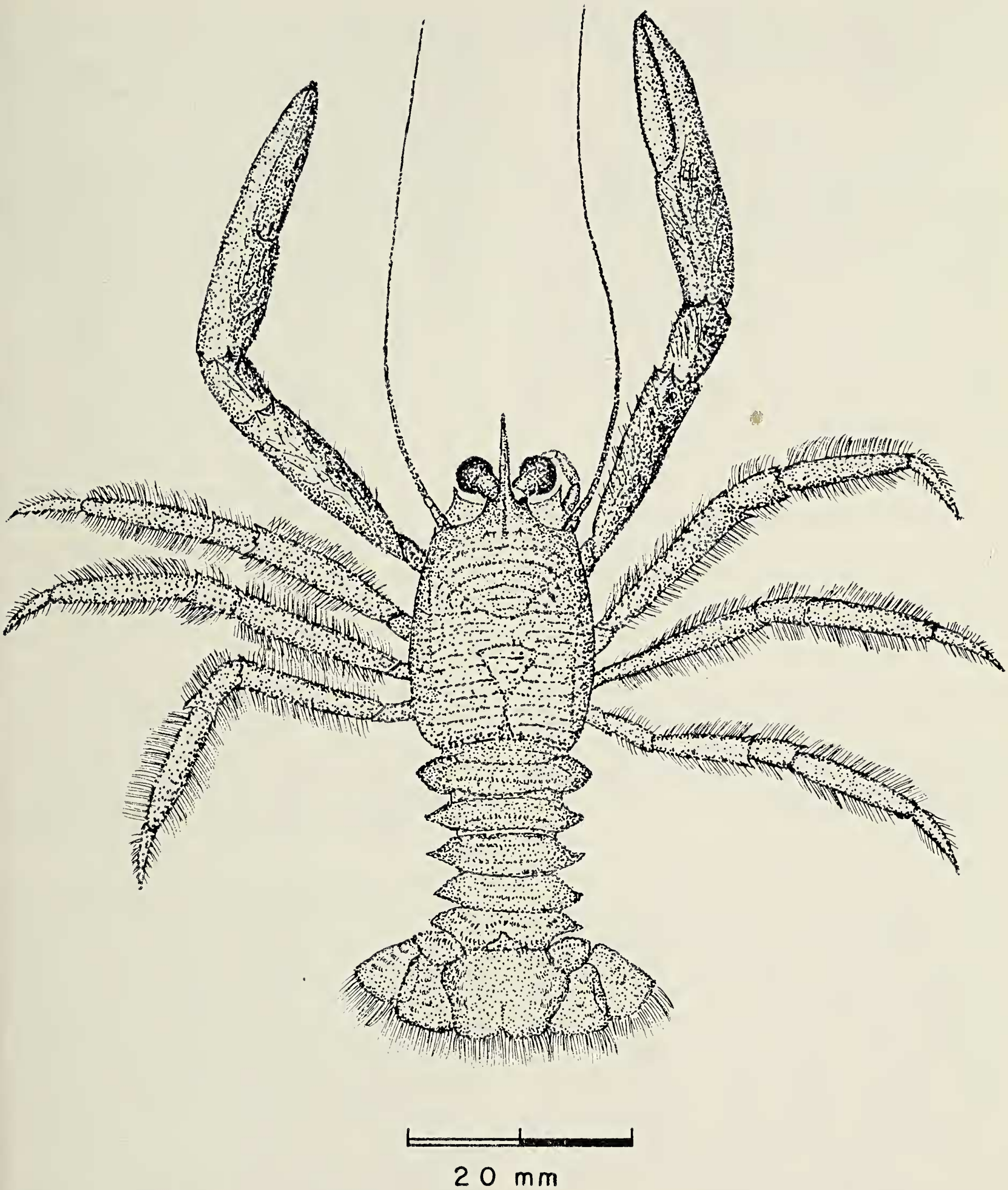

FIG. 1. Dorsal view of a male *Pleuroncodes planipes*. The standard carapace length of this specimen, as measured from the notch between the rostral and subrostral spine to the median dorsal posterior margin of the carapace was 21.3 mm. In life the abdomen is folded under the cephalothorax and the body is bright red.

in aquaria or by experimental work, but only by evidence from the field. The center of the distribution of *P. planipes* in the pelagic phase is off the western coast of southern Baja California. The bright coloration of *P. planipes,* their well-developed eyes, and the known depth distributions of other Galatheidae suggested their occurrence along the continental shelf rather than at abyssal depths. The bottom fauna on the continental shelf of Baja California has been essentially unsampled.

METHODS

A cruise was made to the shelf area of the west coast of Baja California in the region of 26°N in November and December 1960. The following sampling and measuring devices were used at most of the stations occupied: (1) a dredge with a mouth opening 0.5 ft by 2.0 ft; this device was designed to remain closed while being raised or lowered (to avoid catching planktonic specimens), but to open upon contact with the bottom; (2) an otter trawl with a mouth 10 ft wide; (3) a series of plankton nets 1 meter in diameter which were towed horizontally, with one net close to the bottom, another intermediate in depth, and the third at the surface; the two subsurface nets were rigged with the Leavitt opening-closing device, and were open only while being towed at their specific depths; (4) a 900-ft range bathythermograph; and (5) seven Nansen bottles spaced evenly through the water column; the water from these samplers was titrated by the standard Winkler method for dissolved oxygen content.

THE BENTHIC HABITAT

On November 30, 1960 at the first station (26°02′N, 112°58′W), with a water depth of 58 fathoms, a 15-minute tow of the dredge collected 23 specimens of *P. planipes* mired in a ball of gray mud. The 10-ft otter trawl, towed on the bottom for 25 minutes at the same location, caught about 30,000 crabs. A 10-minute tow with the series of plankton nets caught one crab at the surface and none at the two lower depths. It seemed that *P. planipes* was abundant in the benthos.

During the cruise 19 one-meter net tows (each of a single net) were made at different depths at various times of day and night; 13 stations were occupied. After sampling at the first station the time of the plankton tows was lengthened to 20 minutes; each net strained about 800 m^3 of water. A total of seven crabs were caught in these plankton tows. The otter trawl, towed for 25 minutes at each station, probably strained no more than five times as much water as the meter net, but caught hundreds of crabs. The difference in catch between the plankton net and the trawl was so great it seems likely that all of the crabs caught in the otter trawl were benthic, even though the trawl remained open while it was being raised and lowered. This was substantiated by results obtained using the open-closing dredge which, with an opening only 12% of that of a meter net, caught several times as many crabs.

A transect of 5 stations was made across the continental shelf from a point 26°25′N, 112°30′W, along a course 210° true; the western-most station was 85 nautical miles from shore. The substrate on the shelf ranged from gray muddy sand to gray mud, and gave way to naked rocks with solitary corals and crinoids on the continental slope. Crabs were found abundantly on the bottom between depths of 75 and 300 m. Figure 2 presents the distribution of crabs and hydrographic data along this transect. Other stations occupied during the cruise supported the general picture. No crabs were caught on Uncle Sam Bank, which is rough and rocky, nor were any caught by trawls on subsequent cruises at the base of the continental slope in that area, at depths of 1,700 fathoms, where the sediment is again fine.

Other samples were taken on the shelf from 25°N to 31°N, but no crabs were found north of Punta San Eugenio (27°50′N). Trawls towed on a subsequent cruise in April 1961 showed the crabs to be present on the shelf at 24°N. It is probable that they occur southward to the tip of the Baja California peninsula. The benthic distribution in the Gulf of California is completely unknown, but the crabs have been seen at the surface in the Gulf and also have been washed ashore there in great numbers. It is possible that a benthic population exists in areas of the Gulf where the proper depth and substrate occur.

Considerable numbers of two other species of invertebrates were collected with *P. planipes*. One of these was the holothurian (2 cm long), *Cucumaria chilensis* Ludwig, identified by Elisabeth Deichmann of the Museum of Comparative Zoology, Cambridge, Massachusetts.

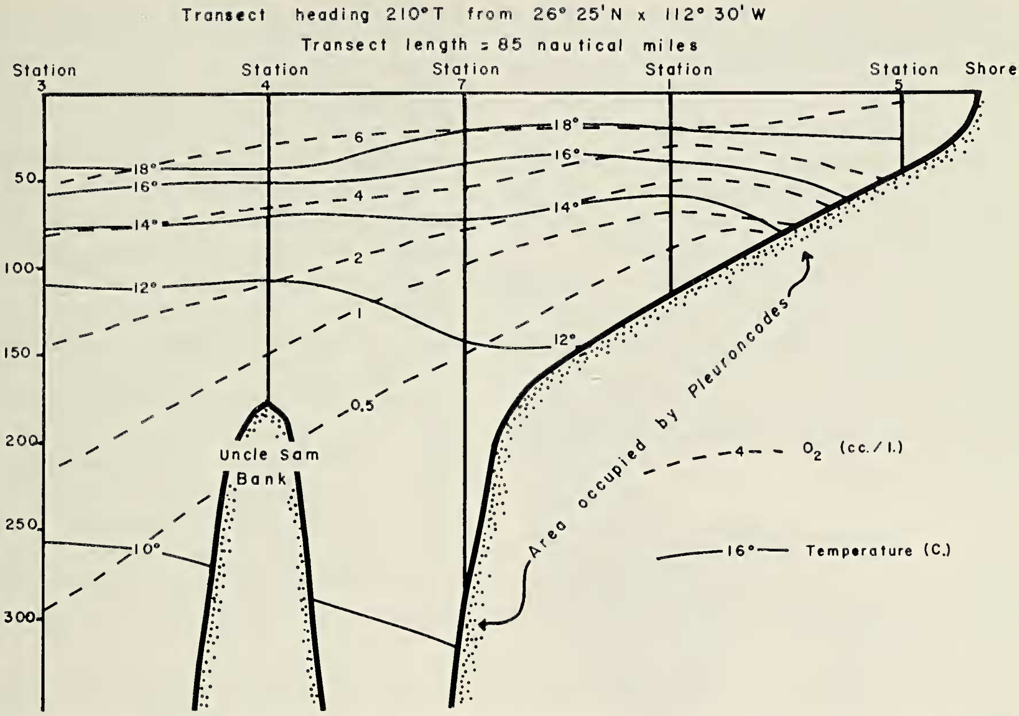

Fig. 2. Vertical profile showing bathymetry, temperature structure, oxygen concentration and distribution of *Pleuroncodes planipes* on the western coast of Baja California, Mexico, in December 1960.

P. planipes, a voracious omnivore, did not eat the holothurians when placed with them in shipboard aquaria (although the crabs would eat pieces of fish under similar circumstances). The other abundant invertebrate was a gastropod, *Nassarius miser* Dall, identified by Emery P. Chace of the San Diego Museum of Natural History. There were very few worm tubes or other obvious animals in the bottom sediment. It is possible that the constant sifting of the substrate by *P. planipes* in their search for food (Nicol, 1932) would reduce the numbers of any invertebrate animals having no defense against the crabs.

No crabs larger than 26 mm in standard carapace length (as measured from the notch between the rostral and subrostral spine and the median posterior margin of the carapace) have been found in plankton collections, and it has been assumed that this was their maximum size. However, at station 7 (depth about 300 m, see Fig. 2) the otter trawl and the closing dredge brought up crabs with a mean standard carapace length of 27.9 mm, and a maximum standard carapace length of 32.0 mm. Juxtaposition of this size on a calculated growth curve (Boyd, 1967) suggests that these larger crabs living along the edge of the continental shelf constitute an older year class; they have probably completed their second year of life. Since no individuals of this size have been taken in the plankton, they are presumably exclusively benthic at this age. Station 7 was the deepest station from which crabs were dredged from the bottom. The mean length of the crabs caught from this deep station differed significantly ($p < 0.05$) from the mean lengths of crabs dredged from other stations, where the means did not differ from each other.

It appears that *P. planipes* lives to some extent on the bottom in its first two years of life and is also found as a planktonic animal at this stage. The relative amount of time spent in these two environments is unknown, but data from plankton collections indicate that there is some diurnal exchange between them, with crabs occurring in the surface water at night and settling to greater depths and perhaps to the bottom during the daytime hours (when a suitable bottom is available). After their second year of life the crabs assume a strictly benthic existence and become segregated from younger animals by assuming a deeper environment.

The number of crabs per square meter of bottom may be roughly estimated by regarding the 10-ft otter trawl as a quantitative sampling device. At one station the trawl was towed for 25 minutes at two knots; it should have swept an area of 50,800 ft.[2] The weight of the catch of crabs was estimated at 400–500 pounds. Since 100 crabs of the size caught in the trawl weighed 0.96 pounds, it is estimated that there were 0.8–1.0 crabs per ft^2 of bottom, or 9–11 crabs per m^2. Estimated densities for other stations were similar.

PELAGIC DISTRIBUTION

The center of the pelagic distribution (region of greatest abundance of crabs), as delineated by data from the numerous plankton tows of the California Cooperative Oceanic Fisheries Investigations and miscellaneous cruises from Scripps Institution of Oceanography, is on the continental shelf of the western shore of southern Baja California. Presumably the crabs are distributed from this population center by the influences of the oceanic current systems. The surface circulation along the western coast of Baja California (Fig. 3) is complex, but in general there are two currents, acting in opposite directions (Reid, 1960). The more obvious of these is the California Current, which sweeps in a southerly direction along the California coast and swings westward in the latitude of southern Baja California. Its hydrography and fauna change gradually, and eventually it becomes or joins the North Pacific Equatorial Current. The effect of this southwesterly swing of the California Current on the distribution of *P. planipes* can

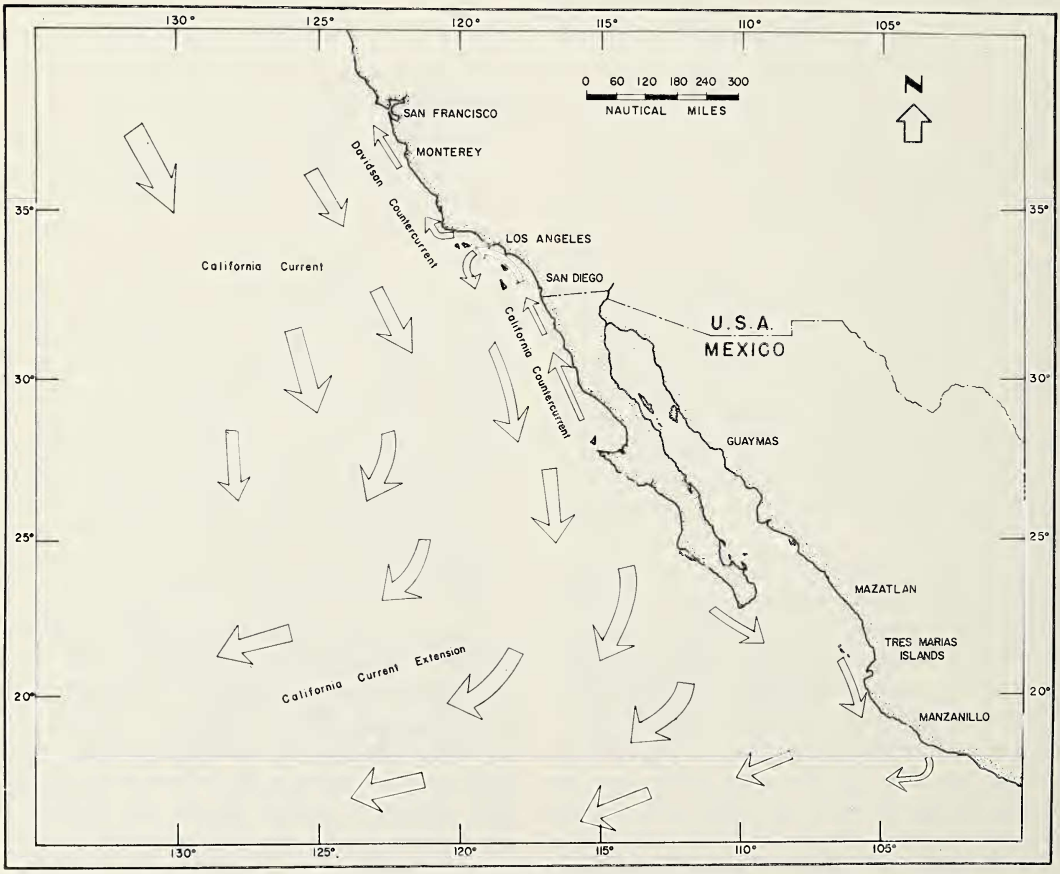

FIG. 3. A schematic presentation of the currents along the coast of California and Baja California.

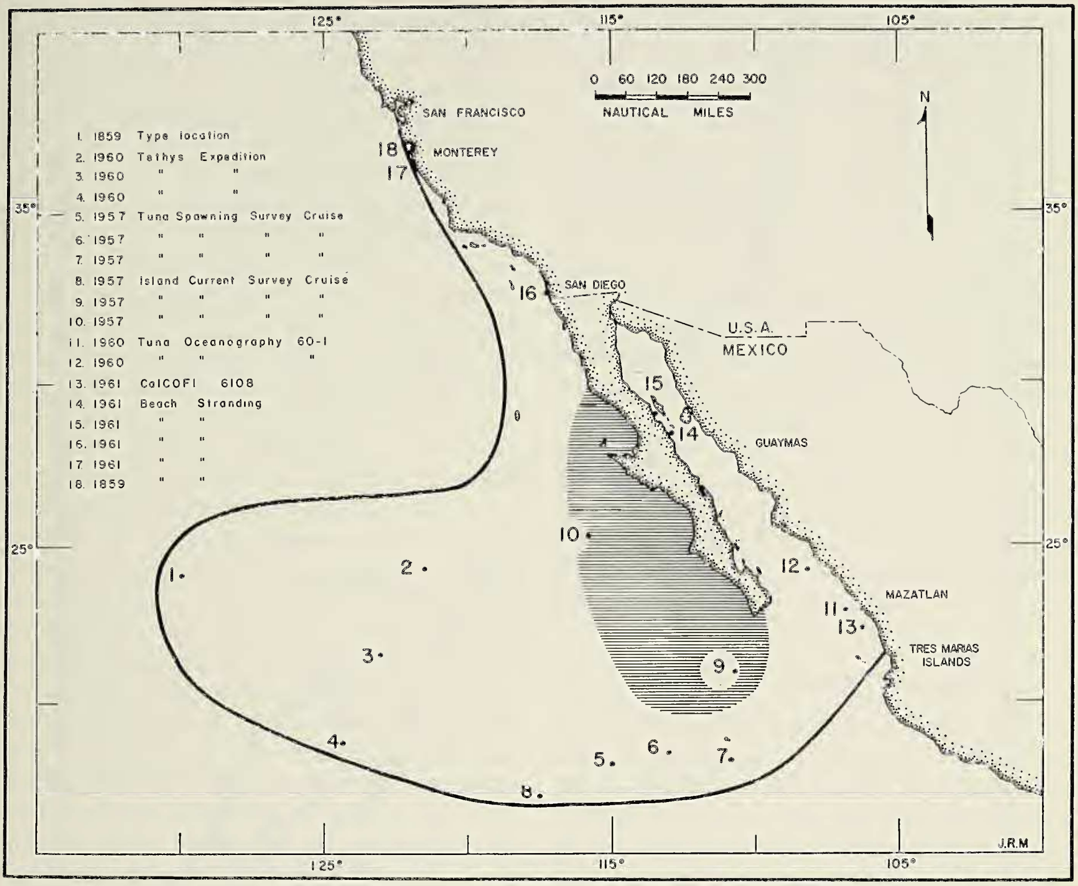

Fig. 4. Chart of outlying occurrences of *Pleuroncodes planipes* and the limits of distribution of the species. The *shaded area* indicates the region of greatest abundance.

be seen by examining Figure 4, which indicates the known range of the species. The westernmost record is from the original species description by Stimpson (1860), at 24°N, 130°W, and is well within the North Pacific Equatorial Current. The few specimens that have been found in the western part of the range probably were swept away from coastal waters. These animals, caught in the Equatorial Current, may be assumed to be expatriates which do not contribute further to the maintenance of the species.

The occurrence of *P. planipes* north of its center of distribution depends upon a system of northerly-moving countercurrents. This system is composed of three parts which may have a common origin (Reid, 1960): (1) the Davidson Countercurrent, which flows northward very close to shore between Point Conception and the Oregon-Washington area; (2) the Southern California Countercurrent, which moves nearshore water northward from southern Baja California and expands into a gyre inside the islands off southern California (Johnson, 1939), and then moves northward very close inshore around Point Conception; and (3) an undercurrent which transports deeper waters (at about 200 m depth) northward from Baja California. The undercurrent is the least understood of the three. The surface countercurrents are known to be seasonal, and have their strongest northward flow in January and February. These countercurrents account for the strandings of *P. planipes* at Monterey, California in March 1959 and again in January 1960.

The distribution of *P. planipes* in February 1960 (Fig. 5) is drawn from analysis of plankton samples taken by the California Cooperative Oceanic Fisheries Investigation's cruise

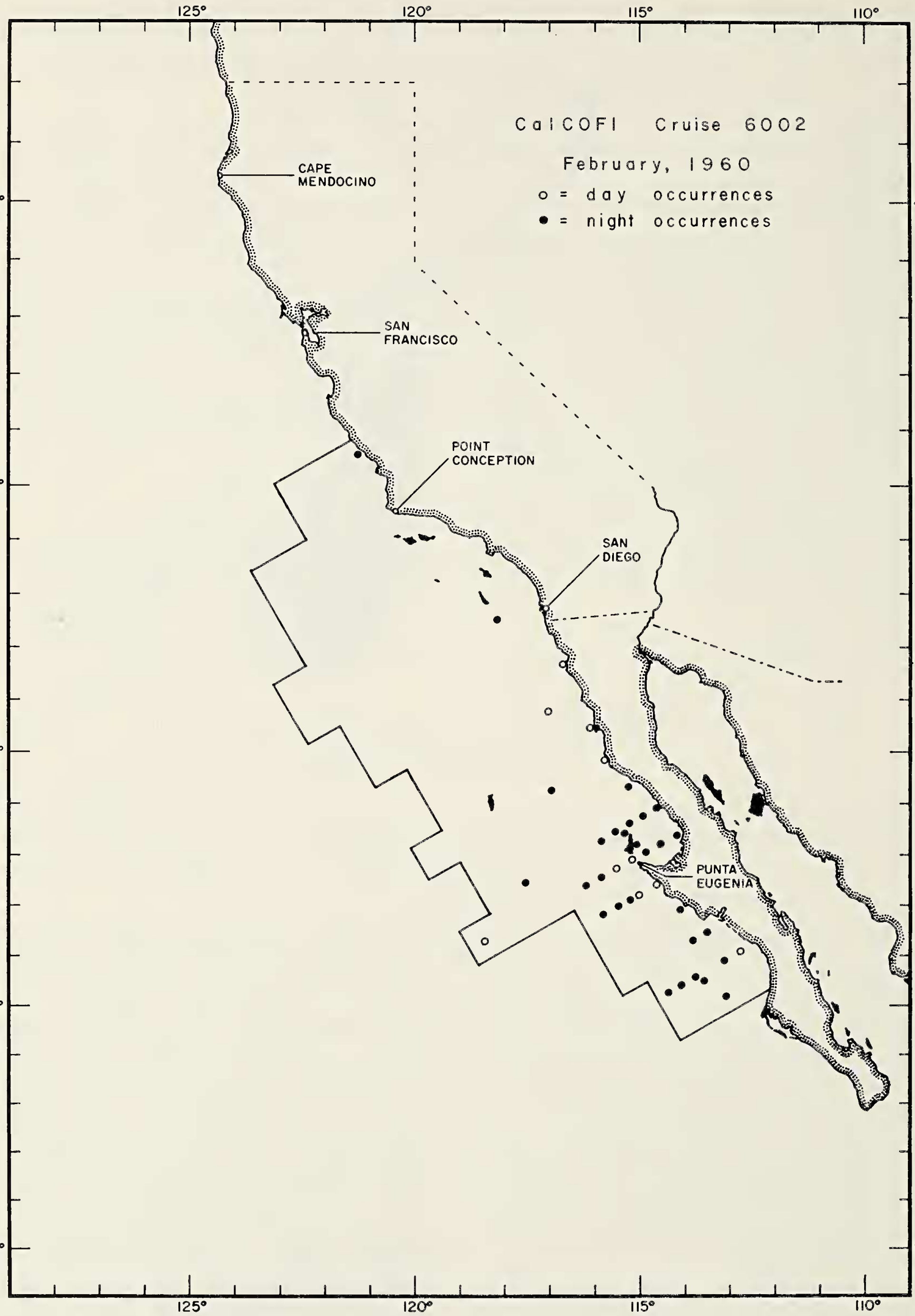

FIG. 5. Occurrences of *Pleuroncodes planipes* on CCOFI cruise 6002, February 1960. Oblique plankton tows from 140 m to the surface were taken with a meter net at stations about 40 miles apart on a grid plan. The area sampled is enclosed by the black line. Daytime captures are shown with an *open circle,* nighttime captures with a *closed circle.*

6002. The specimens captured just south of Monterey represent the most northern intrusion of the animals during the period 1955–1960, and their occurrence in the plankton coincides with their stranding on the beach of Monterey in January 1960 (Glynn, 1961). The period between 1957 and 1960 was noted for the intensification of the countercurrent system and the intrusion of many southern forms into northern waters (Radovich, 1961).

The pelagic distribution of *P. planipes* in the Gulf of California is less well documented because only occasional cruises have been made there. The available data indicate that the crabs sometimes occur in abundance; for instance, large shoals of crabs were sighted in the northern half of the Gulf during the Vermillion Sea Expedition of the Scripps Institution of Oceanography in 1959. The crabs may have been swept in from areas on the western side of the peninsula as a consequence of the sporadic exchange of water between the California Current and the Gulf of California (see charts by Cromwell and Bennett, 1959). The alternative explanation is that the crabs were from a permanent population, even though the benthic habitat probably is very limited; the continental shelf is almost completely lacking in the Gulf, and the shore line drops off precipitously to depths of many hundreds of fathoms.

P. planipes has been captured more frequently during night hours than during daylight hours in the plankton tows of the CCOFI Cruises. In the monthly cruises 6001 to 6008 (January to August 1960), a total of 1,237 plankton tows were made within the region where *P. planipes* might be expected to occur; 601 were made at night and 636 in the day; 197 nighttime stations and 94 daytime stations yielded crabs. When these data are analyzed by 2×2 contingency analysis, the probability ($p < 0.01$) indicates higher nighttime capture. This analysis compared only positive and negative plankton tows and neglected the numbers of individuals caught. This information substantiates the picture of greater nighttime capture; during the March cruise (6003), 536 crabs were caught at night and only 96 in the daytime (the number of stations occupied at night was 71, and by day, 64). A chi-square test of the numbers of crabs caught at the hourly intervals contrasted with the numbers expected at these hours if the crabs had occurred with the same frequency at all times indicates a highly significant difference in frequency ($p < 0.001$). This difference is due to the vertical migration of the crabs to the surface waters at night. The possible explanation that the crabs are avoiding the net during the day is rejected from analysis of a multiple linear regression (Boyd, 1967), indicating that larger crabs were caught during daylight hours; if the day-night abundance differences were due solely to avoidance, the larger animals presumably would have been able to avoid the net more easily than the small animals. While there is a tendency toward upward nocturnal migration it is by no means inviolate; crabs have often been sighted at the surface during the day. It is believed that in neritic waters the animals may settle to the bottom during the day when a suitable substrate is available.

SWARMS AND BEACH STRANDINGS

At times great numbers of red crabs are seen swimming at the surface of the ocean, particularly in the area along the western coast of Baja California. The late Bell M. Shimada of the Inter-American Tropical Tuna Commission reported (personal communication) steaming through such numbers that the "ship seemed to crunch through them for at least ten miles." Concentrations in excess of 100 crabs/m^2 of water surface over broad areas have been seen and photographed, but concentrations of 1–10 m^2 are more common. Reports by many individuals indicate that surface swarms may be sighted throughout the year, both night and day; the occurrence of the swarms does not seem to be associated with seasonal (winter) breeding cycles.

Mass mortalities of the crabs result when the swarms are washed up on the beach; it was such a stranding at Monterey, California in the winter of 1858 that resulted in the description of the species by Stimpson (1860). Many strandings were noted in 1958 and 1959 in the San Diego area, where the crabs had not been sighted in many years, and strandings on the beaches south of Punta San Eugenio are common.

All the crabs involved in the strandings that author has observed have been in the upper 50 cm of water in the surf zone. According to Inman and Quinn (1952) there is a net transport of this surface layer of water onto a beach with breaking waves. This onshore transport is balanced by water moving offshore in fast-moving rip currents and also along the bottom. The beach, then, is the ultimate destination of any object floating in the near-shore surface waters. An onshore wind and a receding tide hasten and intensify the stranding. The number of crabs involved in the strandings may be very large; one report (by George E. Lindsay, Museum of Natural History at San Diego, California, personal communication) from the Gulf of California notes the crabs occurring in windrows up to 3 ft deep and 10 ft wide over a stretch of beach 3–4 miles long.

PREDATORS

Presumably, when the crabs are in the pelagic phase they are preyed upon by large oceanic game fishes, notably albacore, yellowfin tuna, and skipjack tuna; these animals are not known to be bottom feeders. Alverson (1963) indicated that *P. planipes* constituted 78.1% of the volume of the yellowfin tuna's stomach contents in the area along the western coast of Baja California (approximately the area shaded in Figure 4). Around Alijos Rocks (24°57′N, 115°45′W) the percentage was as high as 97.5. *P. planipes* amounted to 34.1% of the volume of the stomach contents of all the yellowfin tuna caught and sampled in the entire eastern Pacific Ocean, and occurred in 39% of the stomachs which Alverson examined. He noted that *P. planipes* was also a significant food item for skipjack tuna as well as yellowfin tuna. McHugh (1952) found *P. planipes* comprised about 11% of the total volume of the contents of the albacore stomachs examined in his study; the percentage was higher (13–43) for those albacore which had been caught in areas where crabs were more abundant.

J. C. Quast (personal communication), in a survey of food habits of common kelp-bed game fishes along southern California, noted that these fishes were feeding on *P. planipes* during the time of his study (1959). Among those fishes were kelp bass (*Paralabrax clathratus*), sheeps-head (*Pimelometapon pulchrum*), various rockfishes (*Sebastodes* spp.), senorita (*Oxyjulis californica*), and sculpin (*Scorpaena guttata*). Yellowtail (*Seriola dorsalis*) and white sea bass (*Cynoscion nobilis*) have been found to feed on *P. planipes* at the Coronado Islands, Baja California, Mexico. Bottom-living fishes are also known to feed on *P. planipes*; boccacio (*Sebastodes paucispinis*), the barber-pole fish (*S. rubrivinctus*), lingcod (*Ophiodon elongatus*), and various other species which had been feeding on *P. planipes* have been caught off La Jolla, California, at a depth of 330 ft.

SUMMARY

Pleuroncodes planipes has been found to exist as a benthic animal on the continental shelf of western Baja California, south of Punta San Eugenio. Two distinct populations seem to exist: a group of larger animals in their third year of life, or older, lives on the outer margin of the shelf; inshore of that group lives a population of animals in their first and second years of life. The smaller animals occupy the greater area, and exist in densities of 9–11/m² of bottom. Plankton tows made in this area and elsewhere indicate that the smaller crabs occur pelagically with a marked daily rhythm, being more abundant in the surface waters at night. When the crabs are in the plankton they are dispersed to the north by the coastal countercurrents and to the southwest by the California Current and Equatorial Current. When the crabs are at the surface they are fed upon by the tuna and albacore, and as the shoals of crabs are set on shore by wind and currents they are eaten by near-shore fishes or they may be stranded and die on the beaches.

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